MORPHOLOGICAL COMPARISONS BETWEEN THE OBLIGATE SOCIAL PARASITE, *VESPULA AUSTRIACA* (PANZER), AND ITS HOST, *VESPULA ACADICA* (SLADEN) (HYMENOPTERA: VESPIDAE)[1]

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Introduction

Obligate social parasites (inquilines) show a vast array of be- havioral and morphological adaptations to their unique mode of life (Wilson 1971). The hazards of colony invasion, usurpation, and subsequent subjugation of members of the host colony (queen and/or workers) require special features in order to overcome col- ony defenses and to become integrated within the host's society. Not only do these species have adaptations for colony takeover, but they also lack certain social characteristics, the most notable being the absence of a worker caste.

Such traits are exemplified in the workerless ant inquiline, *Tel- eutomyrmex schneideri* Kutter, that has enlarged tarsal claws and a gaster with a concave venter which enables this parasite to ride on the dorsum of its host (Wilson 1971). Among the parasitic bumble bees (*Psithyrus* spp.) a number of characteristics, such as strong development of the sting and exoskeleton, are adapted for success- ful colony takeover, while other social traits, such as a pollen- collecting apparatus on the hind leg, are lacking (Alford 1975). Similarly, vespine inquilines are distinct from their hosts in possess- ing stronger exoskeletons, a closer fitting of their abdominal seg- ments, stouter and more recurved stings, broader heads, more powerfully built mandibles, and sharp bidentate clypei (Weyrauch

1937, Beaumont 1958). These traits are presumed to function in preventing sting penetration by host defenders and in facilitating stinging or injuring the hosts.

Investigators have noted these unique traits primarily among the European vespine inquilines and their hosts (Beaumont 1958, Bischoff 1931, Carpenter and Pack-Beresford 1903, Eck 1979, Robson 1898, and Weyrauch 1937). One of these inquilines, *Vespula austriaca* (Panzer), has only recently been found in colonies of a Nearctic species [*V. acadica* (Sladen) Reed et al. 1979] and behavioral interactions with members of the host colony have been documented (Reed 1982). Although researchers have discussed the external morphology of *V. austriaca* in relation to the European host, *V. rufa* (L.), no comparisons have been made between the Nearctic host and *V. austriaca.* Consequently, the objectives of this paper are: (1) a morphometric comparison between the *V. acadica* queen and the parasite; (2) descriptions of certain external features such as the stings, mandibles, femora, and abdominal sclerites; and (3) a survey of exocrine glands of the two species.

Materials and Methods

Seven external body parts were measured in pinned specimens of the host queen and parasite using a dissecting microscope equipped with an ocular micrometer. These characters have been commonly used in other biometrical studies of vespid wasps (Blackith 1958, Eck 1979, Eickwort 1969). Specimens were obtained from local collecting sites (Reed 1982) and from several North American entomological museums (Acknowledgements). Measurements of the interocular distance, mesonotal length, hind tibial length, and forewing length followed the description and diagrams of Eck (1979). Also, the length of the front femur was measured from the base to the apex in the same manner as the hind tibial length, while the width was taken at its widest point. Head width was measured in dorsal aspect, behind the eyes along the vertex, and between the upper edges of the genae. The mesonotal length was measured along the midline from the anterior prescutal suture to the posterior transscutal suture. The length and midline width of the first gastral tergum were also determined in dorsal view.

Scanning electron micrographs (SEM) of the sting apparatus of the host and three parasite species were prepared. Dissected stings were

dehydrated in 100% ethanol, critical point dried, and then coated with gold. Photographs of femora and Dufour's glands, which had been preserved in ethanol, were taken using conventional macro-photographic techniques.

Exocrine glands and certain other internal features (e.g., ovaries, ganglia) were examined in specimens preserved for dissection by injecting Kahle's solution under an anterior abdominal tergum until the gaster swelled. Specimens were subsequently stored in 70% ethanol. Seven *V. acadica* queens and 19 *V. austriaca* females were examined to establish the occurrence and size of the 14 known vespine glands (Landolt and Akre 1979). Dissections were conducted using a binocular dissecting microscope equipped with an ocular micrometer. Gland size and conditon were compared with previous measurements (Landolt and Akre 1979). In a few cases, exocrine glands were inspected in freshly killed specimens. Abdominal plates, mandibular features, and front femora were also studied in the preserved specimens.

Results

The morphometric analysis of selected characters revealed that although both species are very similar in terms of overall body size (i.e., as indicated by the width of the mesonotum and gastral tergum I), certain body parts of *V. austriaca* are significantly larger than those of the host (Table 1). The head and interocular distance of the parasite is slightly wider than that of *V. acadica*. The mesonotum of the two species are comparable with only the mesonotal length being significantly larger in the parasite. Also, the length of the hind tibia and the forewing are longer than the corresponding parts in the host, although forewing length is extremely variable in both species. The first gastral tergum, like the mesonotum, only differs significantly in its length.

One of the more unique morphological differences is the larger front femora of *V. austriaca* (Fig. 1). This femur is consistently wider and longer in the parasite females than in host queens. Furthermore, the femur is quite robust in the parasite, while it is slender and more concave on the innner side in *V. acadica*.

Table 1. Measurements of seven external body parts of *V. acadica* queens (N = 57) and *V. austriaca* females (N = 44).

Body part	Mean and standard deviation (mm)	
	V. austriaca	*V. acadica*
Head width**	4.31 ± 0.14	4.09 ± 0.09
Interocular distance**	1.90 ± 0.08	1.78 ± 0.06
Mesonotum		
width	4.91 ± 0.19	4.86 ± 0.19
length**	3.80 ± 0.17	3.67 ± 0.19
Hind tibia		
length**	3.91 ± 0.16	3.45 ± 0.16
Forewing		
length**	13.6 ± 0.50	13.0 ± 0.56
Gastral tergum I		
width	4.48 ± 0.20	4.39 ± 0.19
length**	1.70 ± 0.11	1.41 ± 0.11
Front femur		
width**	0.89 ± 0.07	0.81 ± 0.06
length**	3.16 ± 0.10	2.78 ± 0.10

**Means are significantly different using the t test at 0.01 level of significance.

The mandibles of both species are roughly triangular when viewing the mesal (inner) face. The dimensions of the three sides are approximately the same in each species; however, the mandible of the parasite is more robust, especially at its base. This stoutness is apparent when viewing the ventral edge of the mandible. The ventro-basal area is distinctly wider in *V. austriaca,* and the mesal face lacks the concavity that is typical of the mandibles of the host queen. The mandibles of both species have three primary or marginal teeth along the truncated, cutting margin with two alternating, secondary teeth and a molar shelf behind the margin as is characteristic of vespines (Duncan 1979). Most yellowjackets (including *V. acadica*) also have a rounded projection immediately beyond the notch on the cutting margin (see Fig. 6 in Landolt and Akre 1979, Duncan 1939); however, this projection in *V. austriaca* is pointed and more tooth-like. Thus, the parasite actually has a fourth marginal tooth near the dorsal edge.

Figure 1. Front legs of a *V. austriaca* parasite (left) and *V. acadica* queen (right). The femur of the parasite is thicker and longer than that of the host queen. The black line indicates 1 mm.

The terga and sterna of the gaster of the parasite are more difficult to dissect apart than those of the host. This "tough armature" is often mentioned in regard to vespine parasites. The gastral sclerites appear to overlap very tightly which undoubtedly prevents sting penetration during usurpation attempts. However, the close fitting of the abdominal segments does not appear to be due to a reduction of intersegmental membranes or because of more sclerotization. Instead, *V. austriaca* has better developed muscles (i.e., larger bundles) in the abdominal sterna and terga than are present in the same segments of a *V. acadica* queen. For example, the three pairs of intersternal retractors (Duncan 1939) of a fat-laden, fall parasite are about 1.5 times as wide as these same muscles in a fall *V. acadica* queen. Consequently, this parasite should be able to retract the gastral sclerites more tightly than a host queen.

The stout, recurved sting of vespine parasites is one of the most important morphological adaptation to their mode of life. The two North American vespine inquilines, *V. austriaca* and *Dolichoves-*

pula arctica (Rohwer), have large and highly curved sting shafts in comparison with those of nonparasitic queens such as *V. acadica* (Fig. 2). However, a facultative social parasite, *V. squamosa* (Drury), does not have a recurved sting shaft, but has a large abrupt curve at the distal end (Fig. 2E). *V. austriaca* and *D. arctica* stylets have a similar configuration, except only the extreme tip of the stylet is abruptly hooked (Fig. 2C). However, this condition is entirely lacking in the *V. acadica* queen (Fig. 2D). Both parasite and host have barbs on the sting lancets.

In conjunction with the curved sting, the distal tip of the seventh abdominal sternum of *V. austriaca* turns down more sharply than does the same sternum of the *V. acadica* queen. In addition, this sternum has prominent lateral carinae on the ectal surface, whereas, this ridge is less developed in the host queen. The seventh sternum in *V. austriaca* is a *ca* 0.40 mm longer along the midline than that of *V. acadica*.

The exocrine glands of four late summer and two spring foundresses, and one fall *V. acadica* queen were examined and measured. Thirteen of the 14 known glands in *Vespula* were present, and their size and development fell within the ranges reported by Landolt and Akre (1979). The endostipal gland was lacking. In contrast, only 12 glands were located in two aged and 17 preusurpation, summer parasites since the sixth sternal and endostipal glands were absent. The head glands, except for the hypopharyngeal, were comparable in size to those of *V. acadica* and other vespines (Landolt and Akre 1979). The two distinct clusters of cells of the hypopharyngeal gland were nearly in contact with each other in the center of the suboral plate of the labrum-epipharynx (see Fig. 5, Landolt and Akre 1979). The clusters were on the average larger than those in *V. acadica*, but were usually within the size range found in *V. pensylvanica* (Saussure) (0.03 – 0.8 mm³). However, two parasites had clusters about 0.12 mm³. The thoracic or salivary glands were also present in *V. austriaca* and were similar in size to those in nonparasitic queens.

Although the seventh sternal gland, eighth tergal gland, and poison gland reservoir are similar in size and development to those of other vespines, evident differences exist between the two species in the other gastral glands. The sixth sternal gland and the associated sternal brush (i.e., tuft of hairs) are absent in *V. austriaca*. This gland (but not the brush) is present in *V. acadica*, other members of
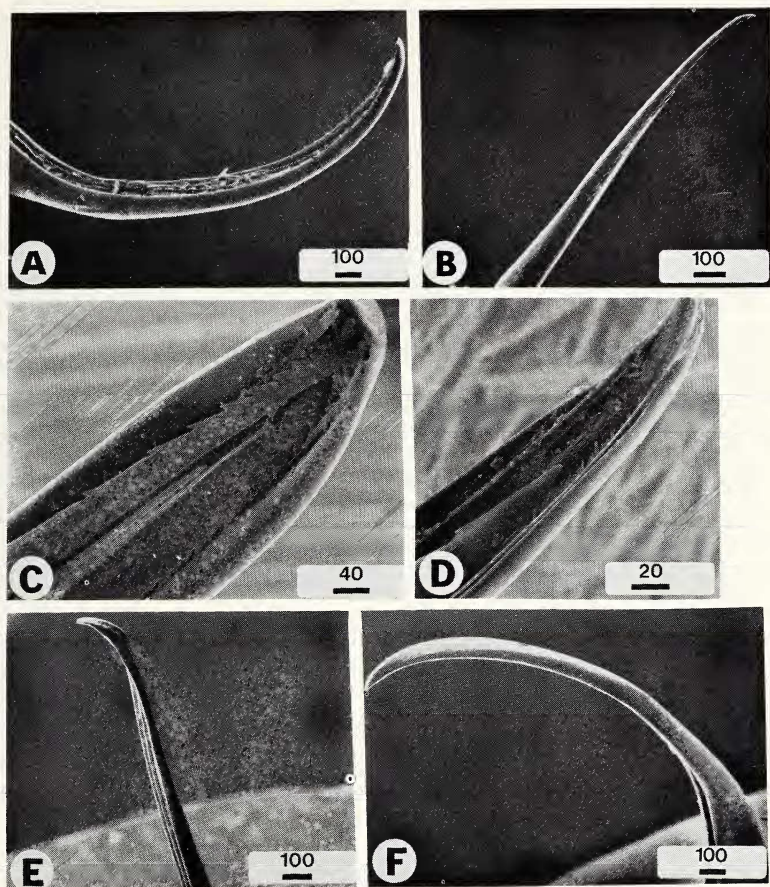
Figure 2. The sting shaft of three social parasites and one host species (*V. acadica*). The sting shaft of *V. austriaca* is larger and curved (A) as compared to the smaller, straight shaft of the host queen (B). In *V. austriaca* the distal tip of the stylet is distinctly curved (C, upper right) unlike the distal end of the stylet in *V. acadica* (D). The facultative, social parasite, *V. squamosa,* does not have a curved sting shaft, but it is sharply bent at the distal end (E). The other Nearctic inquiline, *D. arctica,* also has a recurved sting (F). The measurements are given in microns.

the *V. rufa* species group, and *V. squamosa,* but is absent in queens of *Dolichovespula* and the *V. vulgaris* group (Landolt and Akre 1979). The seventh sternal gland and associated brush are present and well developed in both species. The Dufour's gland of *V. austriaca* is considerably larger than in most other yellowjacket queens (Fig. 3) and averaged 5.8 mm long (range = 4.8 – 7.5 mm, N = 15) and 0.5 to 0.8 mm wide. In contrast, this gland was less developed in *V. acadica* ($\bar{x}$ = 2.1 mm long, 0.3 – 0.5 mm wide) and other nonparasitic queens (Landolt and Akre 1979, 1.5 – 2.5 mm long). The same gland was found to be enlarged in the facultative social parasite *V. squamosa,* as it was *ca.* 0.2 mm wide and 6 mm long (Landolt and Akre 1979). However, the most well developed Dufour's gland is found in the other Nearctic vespine inquiline, *D. arctica.* One *D. arctica* female had a Dufour's gland 14 mm long and 0.3 mm wide (Landolt and Akre 1979) and in two parasites dissected by Jeanne (1977) this gland was 12.8 mm and 27.2 mm long. In this study three, early summer, *D. arctica* parasites were found to have very long glands (16.5, 20.0, 20.5 mm) greatly folded around themselves and the alimentary canal. In these three parasites and 16 other preusurpation individuals the gland was flattened and did not contain any material in the lumen. In contrast, the gland was fully distended and filled with an oily substance in summer, preusurpation *V. austriaca.* It was empty and flattened in new fall parasites, while in the aged parasites the gland was only partially full and appeared collapsed. The gland contained a yellow oily substance in preserved specimens, but instead had a clear, oil-like material in three *V. austriaca* specimens killed and immediately dissected.

The ovaries consist of 12 ovarioles as do most *Vespula* and *Dolichovespula* (Kugler et al. 1976). The ovaries did not fill the entire gaster in the two aged parasites as they did in later summer foundresses of *V. acadica.* Preusurpation parasites and early summer host queens had a slight ovarian development with 1 to 6 eggs greater than 1.0 mm in length and thus probably ready to be laid. Both species have six gastral ganglia.

Discussion

This study confirms the results of a previous morphometric analysis of *V. austriaca* (Eck 1979). Eck (1979) compared the inquiline with the European host, *V. rufa,* and found that although both were
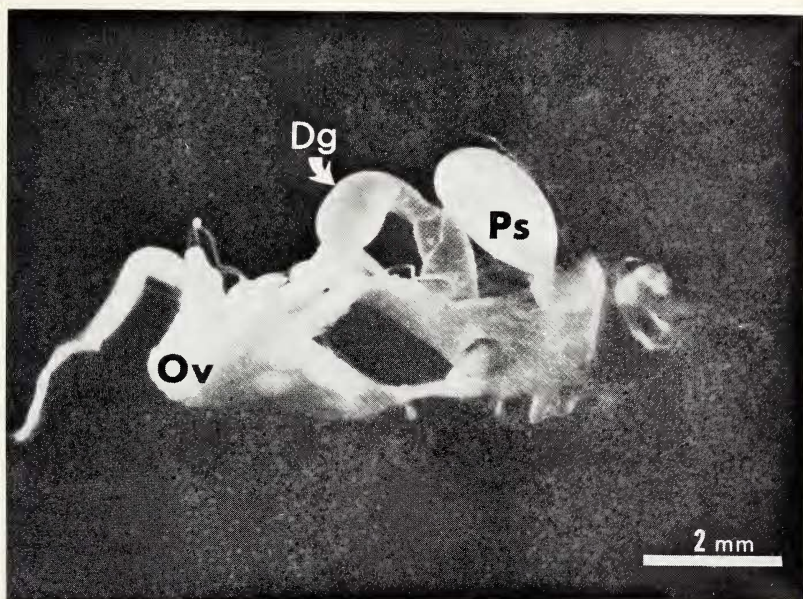
Figure 3. Reproductive organs of a preusurpation *V. austriaca*. The Dufour's gland (Dg) is filled with a clear oil material and was 6.5 mm long when fully extended. Ov = ovaries, Ps = poison sac or poison gland reservoir.

nearly equal in overall body size, *V. austriaca* had a wider head and interocular distance, longer hind tibia, and longer forewing.

Some researchers (Beaumont 1958, Bischoff 1931, Weyrauch 1937) stressed the robust mandible of *V. austriaca,* while others (Bequaert 1916, Carpenter and Pack-Beresford 1903, Robson 1898) found only minor differences in size and did not consider the mandible of *V. austriaca* to be significantly larger. The mandible of *V. austriaca* is definitely robust as it is wider at the base than that of the host. Weyrauch (1937) discussed and diagrammed the robust nature of the mandible of the parasite *Pseudovespula ingrica* (Birula [= *D. ingrica* (Birula)]. He stated that the mandible of the inquiline was less triangular in shape than that of the host queen; a comparison that was not evident in this study. Weyrauch (1937) also illustrated the relatively pointed fourth marginal tooth in *P. ingrica*. The wider head and genae of *V. austriaca* and other vespine inquilines (Bischoff 1931, Weyrauch 1937) undoubtedly house larger mandibular muscles. These muscles in conjunction with the stout mandibles,

make these appendages a formidable, offensive weapon, probably as effective as the sting during colony invasions (Reed 1982). Indeed, Weyrauch (1937) concluded that the powerful mandibles of vespine inquilines were adapted for fighting with the host.

Another adaptation for combat with host queens and defending workers is the enlarged femora of the front legs. The only reference to this feature is found in the original description of *Vespa arborea* Smith (= *V. austriaca*) (cited in Robson 1898) in which he stated that the legs of this species were "stouter and longer" than in *V. rufa*. The robust front legs are not only an advantage during colony invasion, but also are likely an adaptation for the frequent mauling and grabbing of host workers which occurs during early occupation of the colony (Reed 1982).

The sting is greatly curved in vespine inquilines presumably to facilitate penetration between the vulnerable intersegmental membranes of defending colony members. The sharp downward bend of the seventh sternum, likely an accommodation for the recurved sting, was also noted by Bischoff (1931). The abrupt curve at the distal tip of the stylet in the inquilines, as well as in *V. squamosa*, would appear to impede the thrusting of the two lancets. However, the distal end may be curved to hook a sclerite and thus enlarge the intersegmental membrane for further penetration by both the stylet and lancets.

There is no obvious glandular degeneration in *V. austriaca*, but a hypertrophy of one exocrine gland exists. Evidently this enlargement of the Dufour's gland has some role in vespine social parasitism, but unfortunately the function in any vespine is still unknown (Landolt and Akre 1979). Several different functions, such as sting lubrication, have been ascribed to the gland (Spradbery 1973, Maschwitz and Kloft 1971). The secretion is not considered toxic, although Barr-Nea et al. (1976) found some lethality to honey bees. Jeanne (1977) suggested that in *D. arctica* this gland may produce an allomone that has some pacifying effect upon the host queen and or workers. However, the mode of usurpation in *D. arctica* differs from that in *V. austriaca*, suggesting a different function for the gland in the latter. *D. arctica* usually passively invades queen nests and coexists with the queen prior to the emergence of the host workers (Evans 1975, Greene et al. 1978, Jeanne 1977), while

V. austriaca forcibly invades a host colony after worker emergence and does not coexist with the host queen (Reed 1982). Thus, the secretion of the Dufour's gland does not appear to act as a pacifying agent in *V. austriaca* parasitism, and may function as an alarm or dispersing chemical (Reed 1982). The possibility of differing functions of this gland is indicated by the condition of the gland in the two species prior to usurpation. In freshly dissected, preusurpation *D. arctica* parasites the gland was clearly empty, whereas in preusurpation *V. austriaca* females the gland was filled with a clear oil substance. A similar relationship between an enlarged Dufour's gland and social parasitism is found among the slave-making ants of the subfamily Formicinae (Parry and Morgan 1979, Regnier and Wilson 1971) and the dulotic ant *Harpagoxenus canadensis* M. R. Smith (Buschinger and Alloway 1978). In some of these slave-makers the gland discharges a chemical that disperses the defending host workers and attracts other slave-making workers (Regnier and Wilson 1971).

In conclusion, *V. austriaca* possesses morphological features significantly different from the host species. Some, such as the powerful mandibles and front legs, and large curved sting, function as important offensive weapons during colony invasion. Other characteristics, such as the large gastral retractor muscles that enable the parasite to tightly hold the sclerites together, serve as an important defense against stinging host workers. The function of the large Dufour's gland in vespine inquilines remains obscure; however, it probably plays a key role in usurpation and control of the host colony.

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